Fall 2015

Bleaching, disease, and colonization: The ecology of coral health in southeastern Nosy Be, Madagascar

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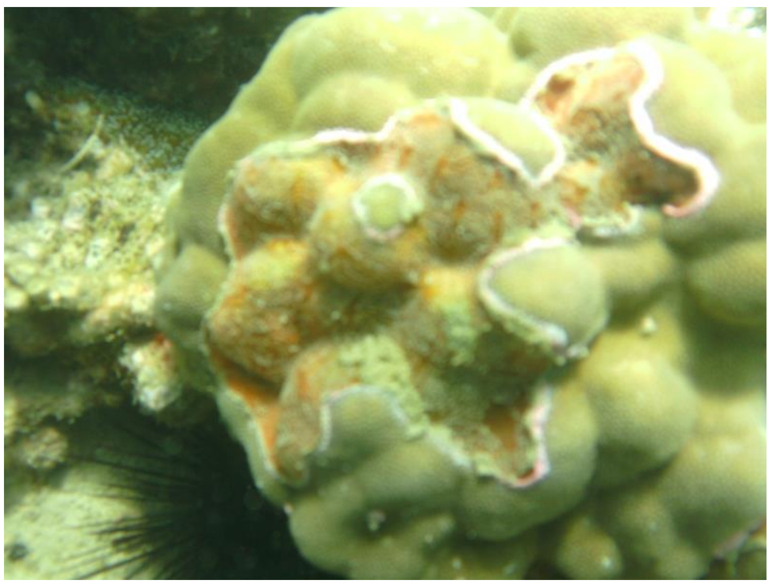

ACKNOWLEDGEMENTS

This study would not have been possible without the consent of Madagascar National Parks, nor without the help, expertise, and hospitality of the Centre National des Recherches Océanographiques (CNRO) in Hell-Ville, including the library staff, administrator and researcher Dr. Jean-Charles Lope, and M. le directeur Jean-Edmond Robilahy. Many thanks in particular to technicians Jacques-Philippe and Octave for their aid and humor in data collection. A special thank-you to my project advisor, head technician Gisèle Bakary, for her extensive knowledge, admirable patience, and open spirit. I'd also like to thank Bemoana for her delicious cooking and her fearlessness during *pindry* attacks. On the SIT side, I am endlessly grateful for the frank advice of our program staff: Jim, Barry, N'Aina, Sôsôny, Mme. Martine, Nadia, and (last but never least) Super Mamy. Finally, all my appreciation to my snorkel partner, roommate, and impromptu barber, Claudia Deeg. In hanger and in health, thank you for the adventures and the laughs.

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ABSTRACT

Coral reefs constitute irreplaceable networks of marine biodiversity as well as an important economic resource to many coastal communities in the tropics. Many factors threaten these fragile ecosystems worldwide: overfishing, pollution, ocean acidification, and increasing sea temperatures all interact to diminish reef-building coral health in a variety of ways. This study aims to characterize the taxonomic and spatial patterns of several acute negative health conditions affecting hard corals in and near Lokobe National Park, Nosy Be, Madagascar. Bleaching, coral disease, filamentous algal overgrowth, and soft coral colonization were surveyed at six fringing reef sites representing different ecological zones. While *Acropora* were most vulnerable to bleaching, *Porites* were most susceptible to coral diseases. No connection was detected between site proximity to freshwater inflow and disease, and no positive correlation was observed between any condition and percent hard coral cover, although sites with the greatest representation of certain genera had higher counts of the conditions affecting those taxa. Overall, sites adjacent to human habitation had the highest rates of all four conditions, confirming that anthropogenic disturbance both on and off the reef itself is likely detrimental to coral health. External environmental drivers' strong influence on coral health highlights a need for holistic conservation approaches in reef management.

INTRODUCTION

Marine biodiversity in Madagascar

Madagascar is well known for its charismatic terrestrial biodiversity, whose high rates of endemism have drawn significant international attention in the form of tourism and conservation alike (McKenna and Allen 2005). Less recognized, but still impressive, is the island's marine life: with over 5000 km of coastline and a wide array of different tropical coastal habitats, Madagascar is thought to possess greater diversity of marine ecosystems than any other country in the Western Indian Ocean (Cooke et al. 2003). In addition to their inherent biological value, this marine life helps to economically and nutritionally support a rapidly increasing coastal population (Bruggemann et al. 2012, McKenna and Allen 2005).

The coral reefs of Madagascar are especially impressive. Recent biodiversity surveys have revealed the presence of over 300 species of reef-building corals, greater than the previous known total for the entire Western Indian Ocean (McKenna and Allen 2005). The island's high diversity of coral and reef invertebrate species is somewhat surprising given Madagascar's distance from the global epicenter of marine biodiversity formed by Indonesia, the Philippines, and Papua New Guinea, known as the "Coral Triangle," and has prompted some to suggest that the scientific community acknowledge a secondary epicenter between Zanzibar, South Africa, and Madagascar (J. Maharavo, *pers. comm*., Oct 2015).

Coral reef ecosystem dynamics

Tropical coral reefs are some of the most complex ecosystems on earth, with a species richness and high diversity of ecological niches surpassed only by tropical rainforests (Longhurst and Pauly 1987). Coral reefs are also home to 25% of the world's total known marine species (Coral Reef Alliance 2014). This species richness is a result of extensive resource partitioning and extremely high rates of symbiosis (Endean and Cameron 1990). Coral reefs have a greater complexity of mutualism and commensalism than is found in any other animal ecosystem. These interactions, built on the exchange of energy and/or nutrients, ensure that these resources remain within the ecosystem. This in turn allows for high rates of biomass accumulation that would otherwise be impossible in the relatively nutrient-poor waters in which reefs thrive (Longhurst and Pauly 1987; Endean and Cameron 1990).

The mutualism between reef-building corals and photosynthetic dinoflagellates is particularly crucial to reef growth. Dinoflagellates, also known as zooxanthellae, are microscopic algae that inhabit the tissues of hermatypic corals (Muscatine 1990). The coral host provides them with nutrients, protection, and a stable position for photosynthesis; in return, the zooxanthellae supply photosynthetically produced sugars directly to the coral tissue and support the calcification of the coral skeleton (Davy et al. 2012). Their omnipresence and autotrophic efficiency make these microscopic zooxanthellae among the primary energy producers of all reef communities (Muscatine 1990). They are also essential to the survival of their coral hosts. Coral polyps feed on zooplankton, but energy flux studies estimate that an exclusively planktonivorous lifestyle would supply no more than 20% of coral energy requirements (Longhurst and Pauly 1987). Therefore, no reef can grow without the maintenance of this mutualism.

This algal-cnidarian symbiosis is a delicate arrangement, however, requiring very specific ecological conditions to thrive. Sufficient sunlight must reach the coral in order for the zooxanthellae to photosynthesize. As a result, coral reefs grow exclusively in clear, fairly shallow waters, and do not tolerate high turbidity. They are also intolerant of salinity below 27%, or temperatures outside the range of 18º-29ºC, as extended periods of thermal stress cause the coral to expel its zooxanthellae in a phenomenon known as bleaching (Longhurst and Pauly 1987; J. Maharavo, *pers. comm*., Oct 2015). There are therefore many environmental factors whose imbalances can undermine coral reef health. However, the very biodiversity that makes coral reefs so complex may also equip them with a high capacity for resilience in the face of new threats (Rogers 2013).

Threats to coral health: interaction and synergy

Periodic natural risks to reef health include earthquakes, cyclones, and volcanic events (Goldberg and Wilkinson 2004). However, the anthropogenic pressures of overfishing, habitat degradation, pollution, ocean acidification, and global climate change together pose mounting threats to reef systems (Obura et al. 2011**;** Rogers 2013). Anthropogenic stressors often work synergistically to decrease coral health, since an initially stressed coral will have less to devote to fighting new stressors (Rogers 2013). For example, high nutrient levels and turbidity due to coastal runoff lower coral tolerance to thermal stress; in this way, terrestrial and marine pollution may render the effects of climate change more severe (Sheridan et al. 2014).

These synergistic environmental effects are particularly important in the case of hard coral diseases, which have emerged as a serious threat to reef health over the past 20 years (Raymundo 2010; Bruckner 2008; Rogers 2013). Generally speaking, coral diseases consist of live tissue damage or death as a result of various pathogenic and environmental disturbances. While coral diseases of the Caribbean have historically received greater research attention, multiple diseases have recently been identified as threats to Western Indian Ocean reefs. These include white syndrome, black band disease, yellow band disease, pink pigmentation response, growth anomalies, skeletal eroding band, *Porites* white patch syndrome, and *Porites* ulcerative white spot (Bruckner 2008; Séré et al. 2015a).

Most coral syndromes are triggered by multiple factors, and the exact causes of many diseases remain unknown (Raymundo 2010). While fungal or bacterial pathogens are often involved, many environmental drivers affect coral susceptibility and pathogen virulence, and therefore the severity of a disease (Harvell et al. 2007; Sweet et al. 2014; Séré et al. 2015b). Higher ocean temperatures, sedimentation, and nutrient enrichment have all been shown to increase the frequency and severity of different disease outbreaks (Harvell et al. 2007; Bruno et al. 2003; Bruno et al. 2007; Sheridan et al. 2014). High coral cover, particularly of a host species, has also been linked with frequency of outbreaks of the Indo-Pacific white syndrome (WS) (Bruno et al. 2007). Meanwhile, reefs in marine protected areas that prohibit fishing show much lower disease prevalence (Lamb et al. 2015; Raymundo 2010).

One almost entirely environmentally triggered condition is coral bleaching, perhaps the most widespread negative coral health response worldwide. Bleaching is the loss of pigmentation after a coral expels its symbiotic zooxanthellae due to thermal stress (usually temperatures in excess of 28-29º C) (J. Maharavo, *pers. comm*., Oct 2015). Bleached corals appear white, since the now-transparent tissue reveals the calcium carbonate skeleton beneath. Since most corals are unable to meet their energy demands from zooplankton feeding alone, bleaching causes colony death unless the photosynthetic symbionts can be recovered (Longhurst and Pauly 1987; Ravindran et al. 2012). Tropical reefs already subsist in temperatures just a few degrees below their lethal limit, and anthropogenic climate change has narrowed or eliminated this already small gap in many places (Harvell et al. 2007). Rising sea surface temperatures over the past two decades have already resulted in a corresponding increase in bleaching. Furthermore, the 2015 El Niño is expected to begin a new global bleaching event forecast to last into 2016 (Goldberg and Wilkinson 2004; Ravindran et al. 2012; Mooney 2015).

Other species' colonization of hard corals can accelerate coral tissue death from bleaching or disease. Exposed skeleton on a hard coral that has already suffered some tissue loss provides a breeding ground for algae or soft coral species. This opportunistic growth inhibits the return of symbiotic zooxanthellae after a bleaching event, assuring the bleached coral will not recover (Ravindran et al. 2012; G. Bakary, *pers. comm.*, 5 Nov 2015). Opportunistic filamentous algae are especially destructive, since an alga established on the exposed skeleton of an otherwise healthy coral can shade and subsequently overtake the rest of the colony, exacerbating the initial degradation and reducing coral polyp recruitment potential (National Ocean Service 2008; Rogers 2013). Soft corals, meanwhile, can exude toxins lethal to hard coral (Longhurst and Pauly 1987).

Local context

The island of Nosy Be, situated off the coast of northwestern Madagascar, has become an increasingly popular international tourist destination (CNRO 2014). However, even as its coral reefs attract amateur snorkelers and divers, the area remains comparatively poorly studied relative to the better-known reefs near Toliara to the southwest (McKenna and Allen 2003). The headquarters of the National Center for

Oceanographic Research (Centre National des Recherches Océanographiques, or CNRO), located just outside Hell-Ville, are therefore ideally placed for the further study of the area's marine ecosystems.

Also nearby is Lokobe National Park, formerly a strict preserve that came under national protection in 2014. A fringing reef surrounds the southern coast of the park and is included in Lokobe's marine protected area (MPA). Twelve freshwater sources drain into the MPA from the forested mountain (Fig. 1). Restricted use of this area is allowed, but the MPA was designated primarily to limit fishing pressure that might degrade the reef (Madagascar National Parks 2014; G. Bakary, *pers. comm.*, 5 Nov 2015). Many of the other fringing reefs of the Nosy Be area remain unprotected and are likely to experience greater fishing pressure as a result.

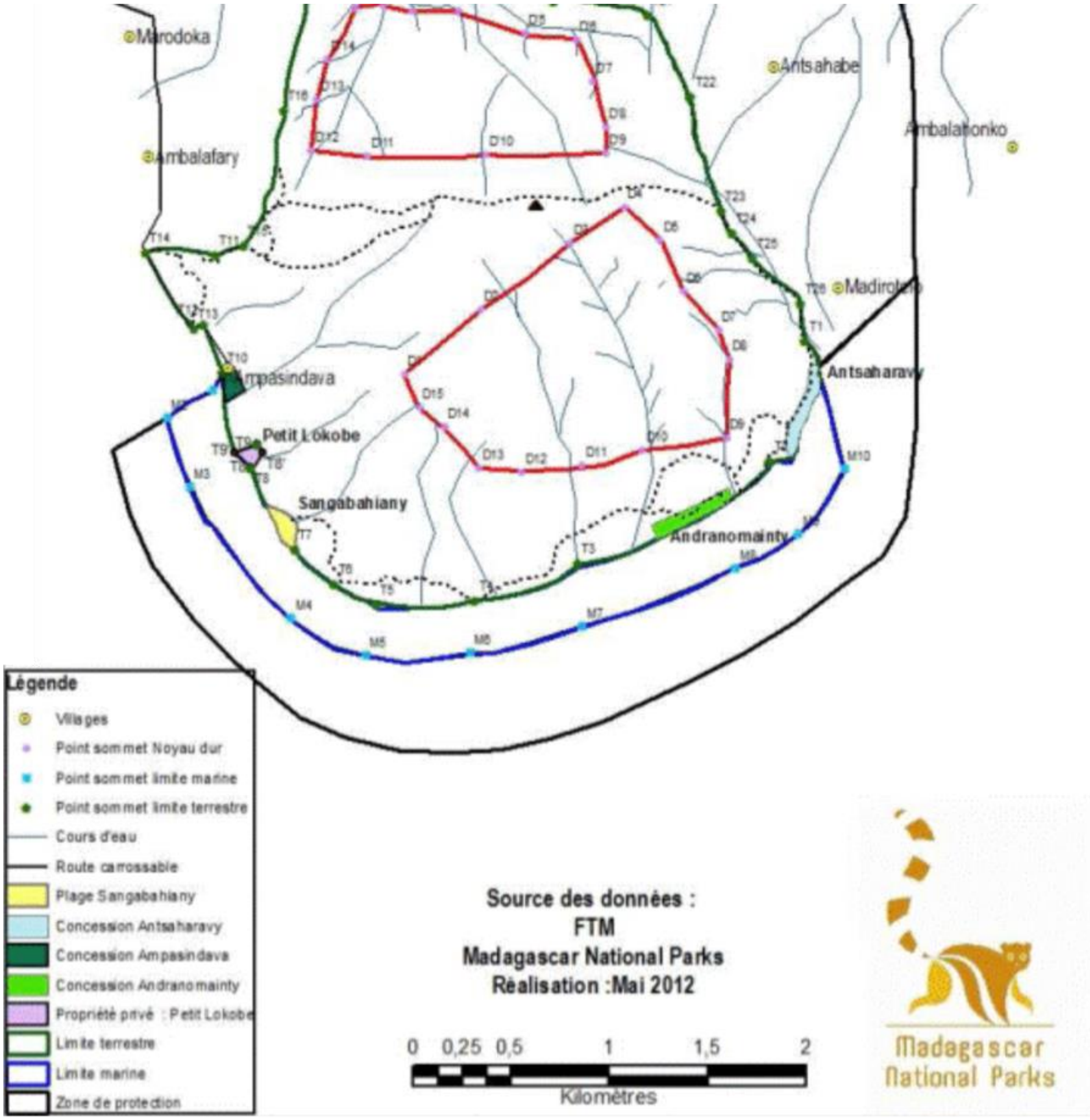


Figure 1. Map of Lokobe National Park and surrounding buffer zone showing villages and freshwater outflows. Outer black line delineates the edge of the protected zone, while inner blue line marks the marine edge of the national park. Map reproduced from “Memorandum Parc National Lokobe,” Madagascar National Parks, March 2014.

Study goals and hypotheses

The present study aims to characterize patterns of several negative coral health conditions across several sites in and near Lokobe National Park in order to better understand the roles that coral composition and various environmental drivers play in disease prevalence in this area. Because anthropogenic factors like pollution and fishing pressure have been shown to increase bleaching and disease elsewhere, it is hypothesized that areas outside the Lokobe MPA and areas closer to human habitation will have higher rates of these conditions (Harvell et al. 2007; Sheridan et al. 2014; Lamb et al. 2015). It is also hypothesized that sites closer to the freshwater outflows of Lokobe will suffer more disease, because sedimentation and low salinity can both increase coral stress and disease severity (Bruno 2003; Sheridan et al. 2014; Longhurst and Pauly 1987). These areas are also likely to exhibit more algal covering, since algae thrive in higher-nitrogen environments (Longhurst and Pauly 1987, Berner 1990). Finally, areas with greater coral cover are expected to have higher disease counts, since they provide a larger host density for opportunistic coral pathogens (Bruno et al. 2007).

METHODS

Station choice and description

Stations were selected after preliminary discussions with CNRO staff and an initial reconnaissance outing in Lokobe. In order to get data on a variety of locations with different ecological statuses, six sites near the CNRO on southeastern Nosy Be were surveyed: five on the fringing reef surrounding Lokobe National Park as well as one reference site on the fringing reef just off nearby Nosy Komba (Fig. 2). All five Lokobe sites were within the restricted use zone of the park's marine protected area. The Nosy Komba site has never been under official protection. Distances to villages and to human habitations varied across sites. All Lokobe sites were near (< 400m away from) freshwater outputs, while the Nosy Komba site was not (MNP 2014; G. Bakary, *pers. comm.*, 20 Nov 2015). Site depths were a maximum of 4 meters, so that detailed data could be obtained from snorkeling (Table 1). All stations were surveyed in mid-November, during the early part of Madagascar's hot and rainy season.

Table 1. Site locations and details relevant to study, as well as conditions at time of data collection (MNP 2014; G. Bakary, *pers. comm.*, 20 Nov 2015; field observations).

Site name	**GPS coordinates**	**Depth (m)**	**Visibility (m)**	**Site details**
Antsaravy	S 13º 25.217' E 48º 19.983'	0-1.5	9	- Lokobe National Park MPA - Freshwater input nearby
Plaque Hely	S 13º 25.467' E 48º 19.433'	0.5-2	9	- Lokobe National Park MPA - Freshwater input nearby
Antsakabagnany	S 13º 25.356' E 48º 18.513'	0-1.5	10	- Lokobe National Park MPA - Freshwater input nearby
Ampasindava Hassanaly	S 13º 24.926' E 48º 18.300'	1.5-2	3	- Lokobe National Park MPA - Freshwater input nearby - Immediately adjacent to human habitation - Adjacent to village
Ambalafary	S 13º 24.501' E 48º 18.092'	1-1.5	2-3	- Lokobe National Park MPA - Freshwater input nearby - No buoys designating protected zone - Immediately adjacent to human habitation - Immediately adjacent to village
Nosy Komba (station: Andrekareka Be)	S 13º 27.084' E 48º 19.666'	1.5-3	5	- Not under protection - Immediately adjacent to human habitation

Figure 2. Map of study area. Stations, and the Centre National des Recherches Océanographiques, appear as stars. The village of Marodoka and the terrestrial Lokobe reserve are also labeled. © 2015 Google Earth.

Hard coral cover and composition

The methodology for evaluating live hard coral cover and generic composition was adapted from the CNRO's benthic survey methodology (CNRO 2014). For each site, four 20-meter belt transects were placed randomly within a 100 m radius of the noted GPS coordinates. Transects were laid using 50-m tape measures secured at both ends to hard substrate. We recorded locations of all substrates and organisms directly beneath the tape measure while swimming each transect. For every hard coral, the form (branching, plate, digital, massive, fan, or encrusting) and genus were also recorded. CNRO staff aided in coral identification. All data were recorded using underwater writing tablets and later transferred to digital logs. Relative abundances of coral genera were then compiled for each site. The percent live hard coral cover relative to other benthos (e.g., sand, herbaceous cover, coral debris, etc.) was also calculated on a site-by-site basis.

Coral bleaching, diseases, and opportunism

Sampling plots for each site were established using the same four randomly placed 20m transects that were used to assess coral biodiversity. Focal areas extended 2.5m to either side of each transect, so that a total area of 400 m^2 was scanned at each station. We surveyed the following hard coral health conditions: bleaching, disease, algal colonization, and soft coral colonization. Eight sub-categorizations of disease were designated according to prior CNRO knowledge, available coral disease handbooks, and literature specific to Western Indian Ocean reefs (Table 2) (Weil 2006, Séré et al. 2015a, Bruckner 2008). The number and category of every health condition were recorded, as well as the genera and form of the affected coral. Data on the genera of corals affected by filamentous algal covering or soft coral colonization were incomplete due to the difficulty of identifying the corals beneath the colonizing entity. CNRO staff aided in the identification of corals and diseases.

Table 2. Abbreviations, categorizations, and descriptions used in the identification of hard coral health conditions observed near Lokobe and Nosy Komba. Descriptions standardized according to Weil 2006 and Séré et al. 2015a. See appendix for examples of selected diseases.

Condition	**Abbreviation**	**Broad disease category**	**Description**
Bleaching	-	-	White, semitranslucent appearance of part or all of a hard coral (no lesions)
Algal assembly covering coral	AA	-	Filamentous algal growth covering partially or completely dead hard coral
Soft coral colonization	-	-	Soft coral growth covering partially or completely dead hard coral
White syndrome	WS	white syndrome	Acute to sub-acute lesions exposing skeleton
Pink spot	PS	pigmentation response	Acute to sub-acute lesions surrounded by a band of bright pink coral tissue
Violet spot	VS	pigmentation response	Acute to sub-acute lesions surrounded by discolored lavender coral tissue
Orange band	OB	pigmentation response	Acute to sub-acute orange lesions
Black band disease	BBD	pigmentation response	Sub-acute lesions surrounded by a band of dark, discolored coral tissue
Yellow band disease	YBD	pigmentation response	Sub-acute lesions surrounded by a band of pale yellow coral tissue
Porites ulcerative white spot	PUWS	other	Multiple small, discrete, acute, oblong white lesions
Tissue necrosis	-	other	Diffuse, somewhat darkened tissue loss with no pigmentation response

To obtain disease rates by site, the numbers of incidents of each disease at each site were divided by the total area surveyed (400 m). Disease abundances were compiled for each site using broad categories (Table 2), while total relative abundances of specific diseases were compiled for Lokobe (sites 1-5) and Nosy Komba (site 6) in order to compare disease diversity. Bleaching and colonization were evaluated on a binary basis (presence/absence) and counts were totaled for each station.

RESULTS

Hard coral cover and composition

The greatest live hard coral cover was observed at Antsakabagnany (70.5%) and Ampasindava Hassanaly (73.53%), while nearby Ambalafary had extremely low hard coral cover (21.98%) (Fig. 3). Ambalafary also showed the lowest genus diversity of any site. *Acropora* was the dominant hard coral genus at every site except for Ambalafary, where *Porites* made up the vast majority of hard corals. *Porites* was the second most abundant genus overall. The relative abundances of other coral genera differed between sites; no other genus was present everywhere, but *Galaxea* and *Echinopora* were both observed at four out of the six sites (Fig. 4).

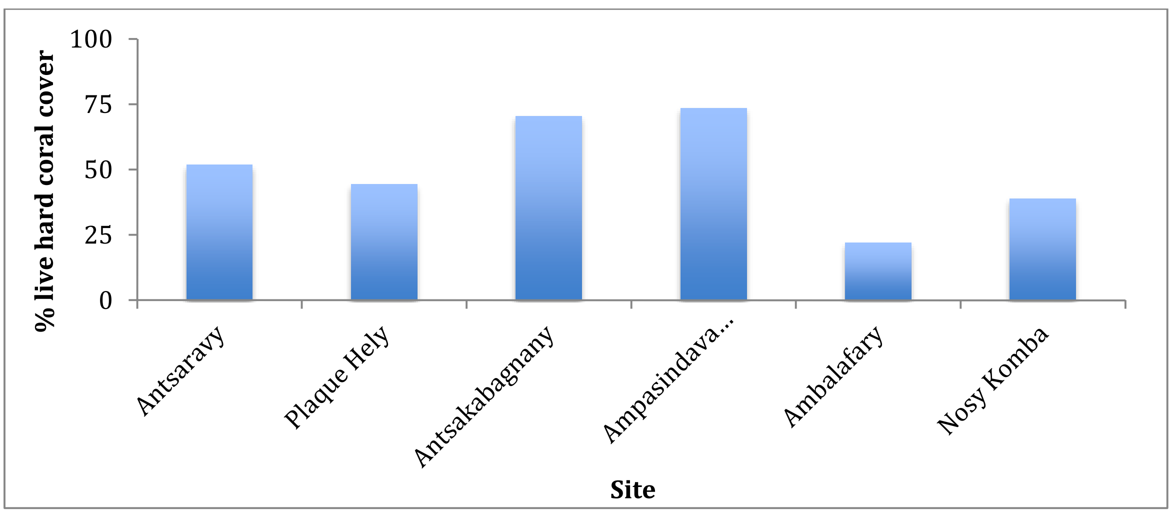


Figure 3. Percent live hard coral cover at each site.

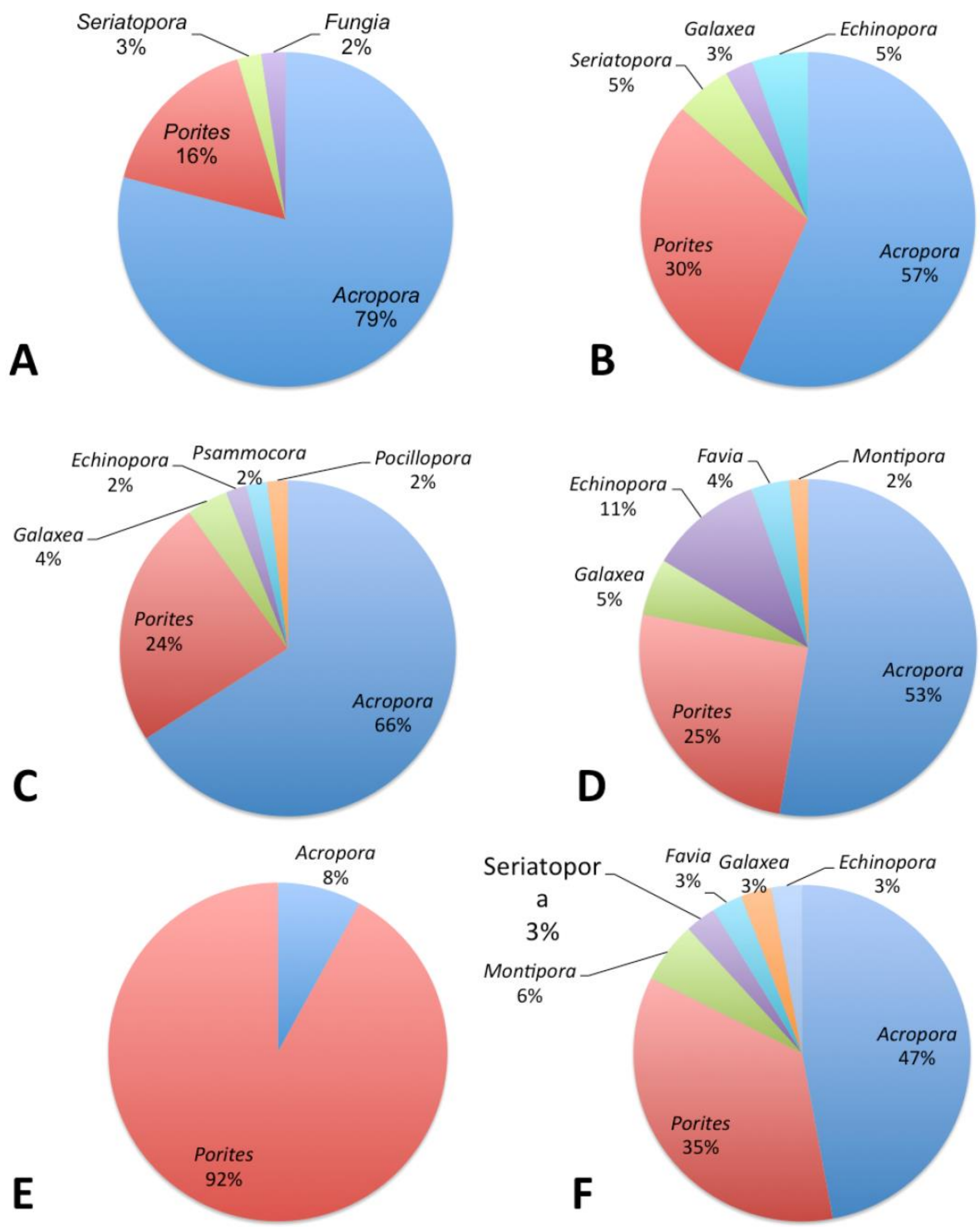


Figure 4. Relative abundances of hard coral genera at each site. A: Anstaravy, B: Plaque Hely, C: Antsakabagnany, D: Ampasindava Hassanaly, E: Ambalafary, F: Nosy Komba

Coral bleaching

Surveys revealed 107 total hard coral bleaching incidents. Bleaching varied dramatically both taxonomically and spatially. Corals of the genus *Acropora* represented 93 of the total bleaching incidents, with *Porites* making up the remaining 14 (Fig. 5).

Much more bleaching was observed at Ampasindava Hassanaly and Nosy Komba (38 and 39 incidents, respectively) than at any other sites, with Antsaravy (4 incidents) and Plaque Hely (5 incidents) displaying the least (Fig. 6).

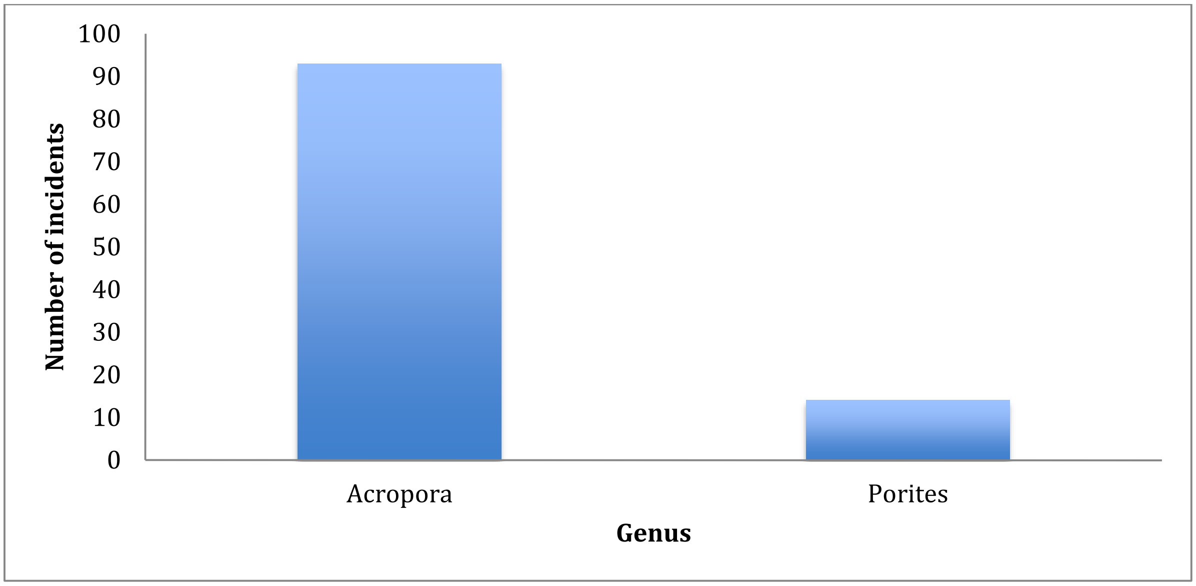


Figure 5. Total incidences of hard coral bleaching by genus, across all stations.

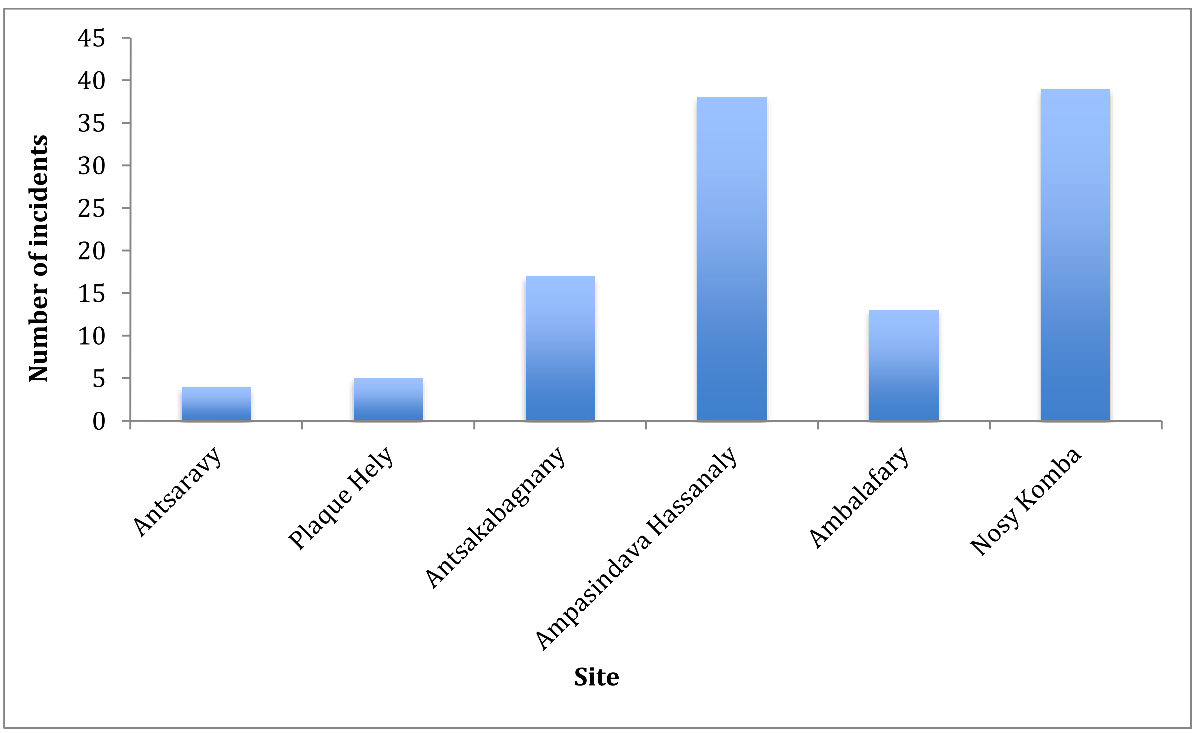


Figure 6. Incidences of hard coral bleaching by station. Area surveyed = 400 m^2 per site.

Coral disease

128 diseased individuals were found in total. Hard corals displaying recognizable disease symptoms fell into two genera: *Acropora* and *Porites*. The vast majority of these were *Porites*, such that nearly all observed diseases (all but 2) affected only that genus. The most common disease was white spot, accounting for 45% of all diseases in Lokobe (stations 1-5 totaled) and 47% at the Nosy Komba site. *Porites* pigmentation responses, notably violet spot and pink spot, were also well-represented (Fig. 7; Fig. 8).

Disease rates varied widely across locations. Nosy Komba had the highest disease rate at 1,075 total incidents/ha, while Antsaravy had the lowest (100 total incidents/ha) (Table 3). Nosy Komba also displayed the greatest diversity of disease; several pigmentation responses not found at any of the Lokobe sites appeared there (Fig. 8).

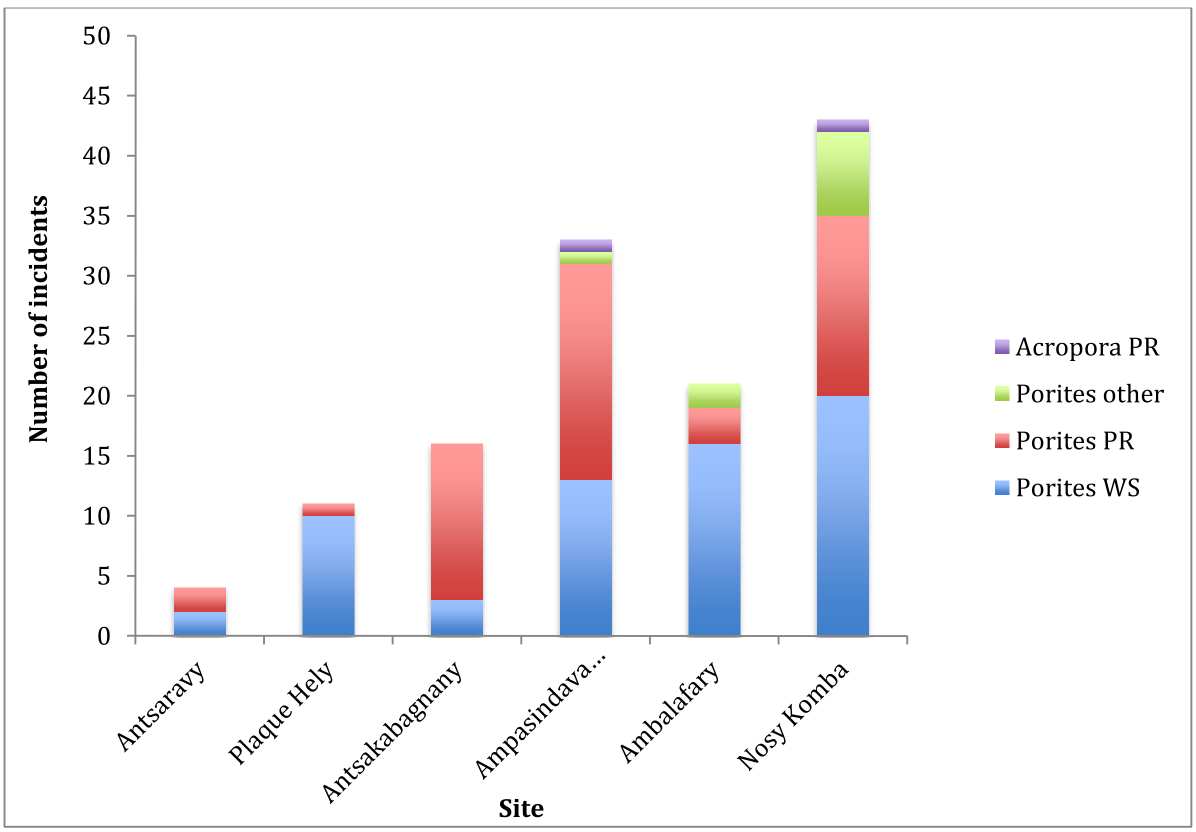
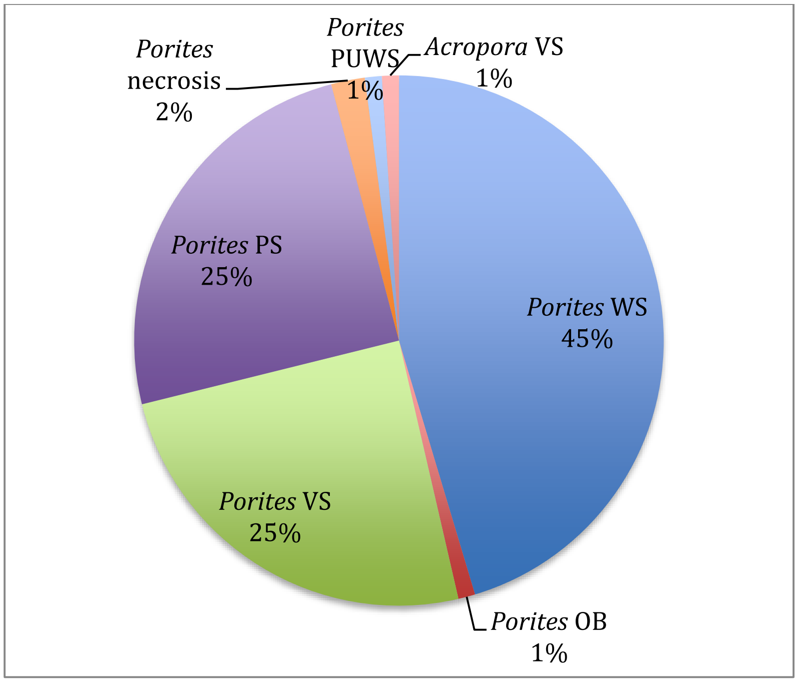


Figure 7. Total incidence of hard coral disease at each site, subdivided by general disease category. WS, white syndrome; PR, pigmentation response.



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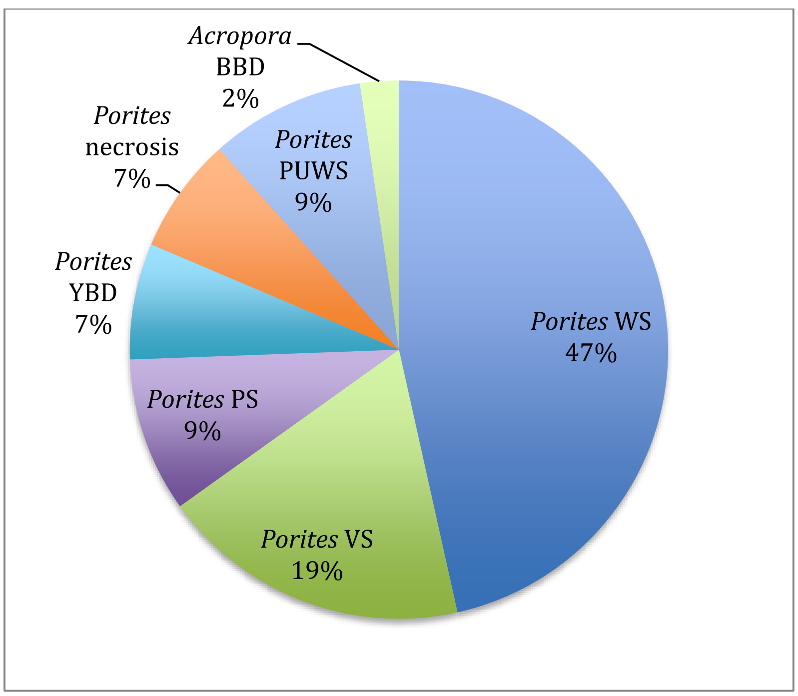

B

Figure 8. Relative disease abundances for (A) Lokobe (sites 1-5 combined) and (B) Nosy Komba (site 6). WS, white syndrome; VS, violet spot; PS, pink spot; YBD, yellow band disease; PUWS, Porites ulcerative white spot; BBD, black band disease; OB, orange band.

Table 3. Rates of incidence for broad categories of disease at each station surveyed. WS, white syndrome; PR, pigmentation response.

Site name	**Total disease (incidents/ ha)**	***Porites* WS (incidents/ ha)**	***Porites* PR (incidents/h a)**	***Porites* other (incidents/ ha)**	***Acropora* PR (incidents/ ha)**
Antsaravy	100	50	50	0	0
Plaque Hely	275	250	25	0	0
Antsakabagnany	400	75	325	0	0
Ampasindava Hassanaly	800	325	450	25	25
Ambalafary	525	400	75	50	0
Nosy Komba	1,075	500	375	175	25

Algal and soft coral colonization

Surveys revealed 109 incidents of filamentous algal assemblage on hard coral. Counts of algal colonization varied across sites and were greatest at Ambalafary and Ampasindava Hassanaly (35 and 33 incidents, respectively) (Fig. 9). 27 hard coral individuals experiencing soft coral colonization were also observed, mostly at Ambalafary (11 incidents) and Nosy Komba (12 incidents), with little to none at most other sites (Fig. 10).

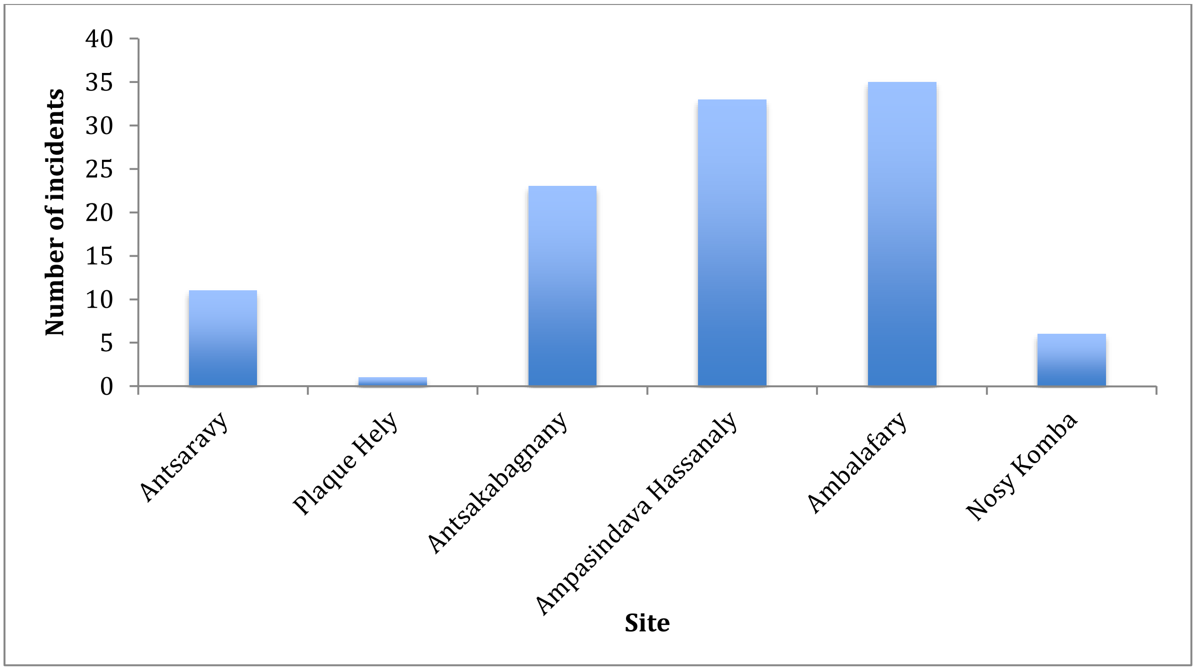

Figure 9. Incidences of algal colonization of hard corals, by station. Area surveyed = 400 m^2 per site.

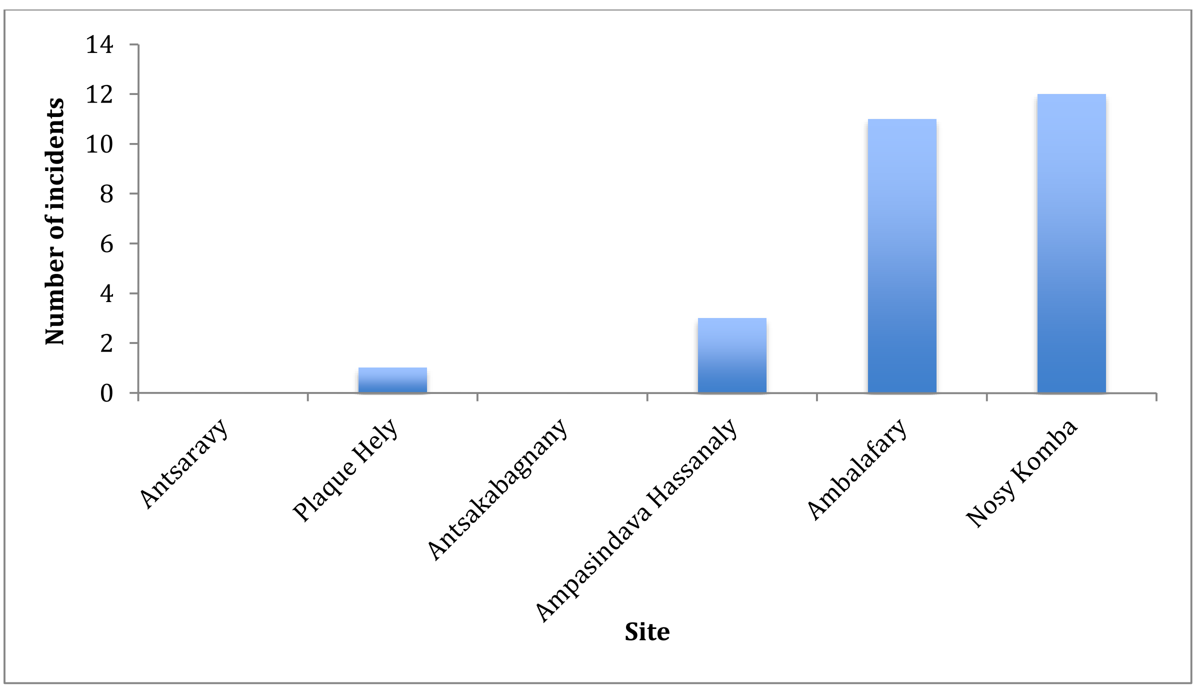

Figure 10. Incidences of soft coral colonization of hard corals, by station. Area surveyed = 400 m^2 per site.

DISCUSSION

Bleaching patterns

Taxonomic variation

The genus *Acropora* was more affected by bleaching than other genera (Fig. 5). Part of this pattern can be attributed to this genus being the most commonly observed genus overall (Fig. 4). However, the relative abundance of acroporid corals cannot fully explain their high bleaching counts: although they made up 55.1% of the total corals noted, they constituted 86.9% of bleached individuals. This overrepresentation indicates that the genus *Acropora* is especially susceptible to bleaching. This study confirms prior Indian Ocean findings that acroporids are more affected by bleaching than non-acroporids, especially in shallow areas such as those studied here (Goldberg and Wilkinson 2004; Hobbs et al. 2015). *Acropora* are thought to be more vulnerable to thermal stress due to their relatively fast growth, which reduces energy availability to the coral immune system (Marshall and Schuttenberg 2006; Séré et al. 2015a).

Spatial variation

Nosy Komba and Ampasindava Hassanaly both had dramatically higher counts of bleached individuals than any other sites (Fig. 6). In light of the taxonomic variation discussed above, we would expect some of the observed spatial variation in bleaching to be due to between-site differences in coral composition: sites with more *Acropora* should be more bleached given this genus's apparent greater sensitivity to thermal stress. However, while Ampasindava Hassanaly does display the highest hard coral cover overall, Nosy Komba had relatively low hard coral cover (Fig. 3). Moreover, both Nosy Komba and Ampasindava Hassanaly had low relative abundances of *Acropora* when compared with other sites (Fig. 4). It is therefore unlikely that bleaching patterns are attributable simply to a greater number of *Acropora* at these sites.

Spatial patterns of bleaching prevalence must then be due to other environmental factors. While the sites are relatively removed from each other, there was evidence of human habitation on the shores immediately adjacent to both Nosy Komba and Ampasindava Hassanaly (Fig. 2; Table 1). Nearby human activities may decrease water quality around these sites, which may be compounded by the effects of freshwater runoff in the case of Ampasindava Hassanaly (Table 1). Long-term increases in seawater turbidity and nutrient enrichment via pollution and runoff have been shown to increase hard coral stress by several mechanisms, thus rendering corals more susceptible to bleaching (Vega Thurber et al. 2014). A coral in turbid water must divert energy to the effort of removing sediment from its surface. Meanwhile, a reduction in water clarity limits the photosynthetic capacity of the symbiotic zooxanthellae, further decreasing host coral energy availability. These stressors in turn reduce the coral's coping capacity for thermal stress, causing it to expel its symbionts and thus bleach more readily (Rogers 2013, Sheridan et al. 2014). Thus, the human habitations in close proximity to these sites may help account for their high bleaching totals. The medium to poor visibility at both sites further suggests that they may experience greater turbidity than the areas around Antsaravy and Plaque Hely to the west (Table 1). However, permanent differences in turbidity are uncertain, since "visibility" is a subjective measurement that also varies with weather conditions.

The shallowness of the bay close to the village might also promote bleaching, since we would expect shallow water to be more sensitive to temperature fluctuations.

However, any thermal differences due to depth are only conjectured at this point. Further research would be necessary to determine whether there is actually any substantial temperature difference between the bay to the west of Lokobe and the channel to the south (Fig. 2).

Given these suspected anthropogenic effects, we would expect higher bleaching totals at Ambalafary, the site closest to Marodoka village (Fig. 6; Table 1). However, the site's low coral cover (Fig. 3), particularly of acroporids (Fig. 4), might account for the low bleaching total there. Despite the inability of taxonomy alone to predict highly bleached areas (see above), it may explain the surprisingly small count in this case. If *Acropora* are especially susceptible to bleaching, as the data suggest, then it makes sense that a site with very few acroporids would display much lower bleaching counts than hypothesized based on external ecological conditions alone (i.e., sedimentation, turbidity, freshwater input, and proximity to human habitation).

Patterns of coral disease

Taxonomic variation

Disease was much more prevalent among *Porites* corals than any other genera. *Porites* are known to be particularly disease-prone, particularly in the Indo-Pacific (Harvell et al. 2007; Carpenter et al. 2008; Séré et al. 2015a). The host specificity of some common coral pathogens may partially explain this effect. The disease referred to as "pink spot" at the CNRO is likely *Porites* trematodiasis, which is caused by the parasitic trematode *Podocotyloides stenometra* and manifests in bright pink nodes on the outside of the coral. Although *P. stenometra* requires multiple hosts over the course of its life cycle, including a mollusk and a corallivorous fish, its second intermediate phase is host-specific to species of *Porites* (Aeby et al. 2007). Similarly, an unidentified species of *Vibrio* (a common marine pathogenic bacterial genus) has been linked with *Porites* ulcerative white spot syndrome (PUWS), so named because it causes isolated white lesions in *Porites* exclusively (Harvell et al. 2007). Pink spot and PUWS are therefore both ecologically limited to *Porites* corals. More generally, the high predation pressure that *Porites* corals face may also be responsible for their proneness to disease. Tissue damage from corallivorous fish renders the surfaces of corals more vulnerable to opportunistic pathogens. Additionally, these fish could act directly as coral disease vectors, worsening outbreaks among their preferred prey (Séré et al. 2015a).

Observed low disease rates on *Acropora* are at odds with some findings from the Eastern Indian Ocean that acroporids are the corals most affected by outbreaks of white syndrome, the most common disease found in this study (Hobbs et al. 2015). It is worth noting, however, that the term "white syndrome" may not refer to the same disease in both cases, particularly in light of the substantial geographical difference between these studies. Due to the numerous as-yet unidentified coral diseases, many researchers use general names for categories of similar lesions. Sometimes the same disease can manifest in various patterns under different circumstances; other times multiple different causes can result in the same observable signs of disease (i.e., spots of white or lost tissue). "White syndrome" in particular has been used to describe several pathologically distinct syndromes (Bruno et al. 2007). Direct comparisons of white syndrome between this and other studies are therefore of limited use until molecular data allows for a more thorough description of the cause(s) of white lesions around Nosy Be.

Variation with coral cover

Contrary to this study's initial hypothesis, percent live hard coral cover proved to be a poor predictor of disease across sites. No correlation was observed between the two variables. While Ampasindava Hassanaly did have notably high rates of both coral cover and disease, the "most diseased" site, Nosy Komba, had the second-lowest coral cover of all locations (Fig. 3; Fig. 7). This result is surprising given previous findings that high coral cover worsens disease outbreaks (Bruno et al. 2007). However, the relationship between the two variables may be more complex than a direct correlation; Aeby (2007) found that levels of infection for *Porites* trematodiasis increased with coral cover up to a point, after which higher coral cover meant a decline in the disease.

One possibility is that those reefs with the greatest coral cover are also likely to have greater coral species diversity, which could slow the spread of diseases specific to one host. Higher cover specifically of host corals is known already to correlate with disease prevalence, particularly with WS and *Porites* trematodiasis (Hobbs et al. 2015, Bruno et al. 2007). This pattern was observed around Lokobe and Nosy Komba as well. Plaque Hely (30%), Ambalafary (92%), and Nosy Komba (35%) had the greatest relative abundances of *Porites* out of all sites (Fig. 4). They also all show relatively high levels of WS in *Porites* (Fig. 7; Table 3). It is possible that disease outbreaks are less severe in locations with greater species diversity, since infections spread more rapidly with denser host distribution (Rogers 2013). Research incorporating an examination of coral biodiversity is required to determine the exact effects of reef composition on the spread of disease.

While percent live hard coral cover is by itself an unreliable predictor overall for disease prevalence, poor coral cover may explain Ambalafary's anomalously low disease count when compared with its neighbor Ampasindava Hassanaly. Ambalafary's disease rates lag behind those of Ampasindava Hassanaly and Nosy Komba, despite its closest proximity to the village out of all sites, as well as the lack of buoys reinforcing protected area limits. We would expect both these factors to increase the site's pollution and fishing pressure, and therefore its disease rates (Sheridan et al. 2014; Lamb et al. 2015). Instead, poor hard coral cover may partially account for this site's lower disease count as well as its low bleaching total (see above) (Bruno et al. 2007; Rogers 2013). The case of Ambalafary thus highlights the importance of understanding a site's benthic composition, as well as any external pressures it might face, in conservation oversight efforts.

Spatial variation

Similarly to bleaching, coral disease tended to be more prevalent at sites closer to human habitation. The three sites with human habitation on the shore adjacent (Nosy Komba, Ampasindava Hassanaly, and Ambalafary) had the greatest disease rates (Table 1; Table 3; Fig. 7). Nosy Komba, the only officially unprotected site, had the highest disease count of all locations by far, as well as the greatest diversity of diseases. This site alone displayed as great a diversity of syndromes as all five protected Lokobe sites combined (Fig. 8).

These results are consistent with the study's initial hypothesis that areas suspected to be subject to greater anthropogenic disturbance would be more disease-prone. Lamb et al. (2015) found that no-take fishing zones had significantly reduced disease rates, likely due to the protection of corals from physical damage that would otherwise render them vulnerable to infection. According to CNRO staff, a lack of official protection around Nosy Komba results in heavy fishing pressures at that location. However, sites in Lokobe closer to the village still suffer illegal fishing activity, especially Ambalafary, where no buoys are in place to mark the limited-use zone (G. Bakary, *pers*. *comm*., 20 Nov 2015). Fishing in these areas may be a part of their putatively anthropogenic high rates of disease.

Another possible driver of disease near human habitations is decreased water quality due to pollution and turbidity. Although reef species are adapted to thrive in an oligotrophic environment, coral polyps feed on bacteria and particulate organic matter suspended in the water; some nutrient influx is therefore beneficial to the system (Longhurst and Pauly 1987; G. Bakary, *pers*. *comm*., 5 Nov 2015). However, overabundances of carbon and nitrogen have been linked to disease outbreaks elsewhere in Madagascar and the world (Bruno et al. 2003; Harvell et al. 2007; Raymundo 2010). Sewage and other anthropogenic pollutants are rich in these elements, meaning that human habitation near reefs is likely to increase disease progression rates (Sheridan et al. 2007). Meanwhile, high turbidity limits zooxanthellate photosynthesis and mandates that corals spend energy on particulate removal, increasing vulnerability to disease just as it may for bleaching (see "Bleaching patterns" above) (Rogers 2013, Sheridan et al. 2014).

While this study cannot distinguish between the effects of these different disturbances, many are likely interacting to make the reefs near Nosy Komba and Marodoka more vulnerable to disease. For example, while there was no evidence in support of the hypothesis that the freshwater inputs of Lokobe increased disease rates there relative to Nosy Komba, it's possible that sedimentation from freshwater input does influence disease prevalence in Lokobe, but that the anthropogenic factors affecting Nosy Komba mask these effects. Further studies separating anthropogenic from natural disturbance could shed light on the precise role freshwater runoff plays in reef health around Nosy Be.

It is important to note that there appears to be a strong relationship between counts of coral bleaching and coral disease (Fig. 6; Fig. 7). Because these conditions both tend to affect different genera, we would expect them to dominate at different sites, depending on where each “target genus” was most plentiful. Instead, the consistency of the spatial distributions of bleaching and disease implies that environmental drivers other than reef composition must have an overpowering effect, causing surges in prevalence of different conditions at the same sites. That these patterns follow one another closely despite taxonomic predictors underscores the interrelatedness of coral health conditions: those already suffering thermal stress are probably less resistant to infection, and vice versa. These compounding stressors are particularly dangerous for reefs and necessitate holistic approaches to reef management that take into account different scales and sources of threats (Rogers 2013).

Patterns of opportunistic colonization

Incomplete data on the genera of corals experiencing colonization by filamentous algae or soft corals makes it impossible to draw conclusions on the variation of these conditions due to taxonomy. However, we can conjecture that the corals most affected by bleaching would also be most affected by algal recovering, since bleached corals are most susceptible to opportunistic growth (National Ocean Service 2008; Ravindran et al. 2012).

Therefore we would expect *Acropora* to make up the majority of corals supporting opportunistic algal assemblages (Fig. 5).

Similarly to bleaching and disease, soft coral growth and algal assemblages seemed to correlate with proximity to human habitation; the relationship is particularly apparent for soft corals (Fig. 9; Fig. 10). One possible explanation is that sites closer to villages or human habitation are more likely to experience physical damage from fishing. This would result in a greater amount of dead coral, which provides a hard substrate ideal for colonization.

A notable exception to this trend is Nosy Komba, which is immediately adjacent to human habitation yet had very little algal colonization (Table 1; Fig. 9). Low counts of algal assemblages may in this case be attributed to the comparative lack of nutrients to the west of Nosy Komba, where there are no freshwater outflows (Gisèle Bakary, *pers. comm.*, 20 Nov 2015). We would expect more algal assemblages in areas experiencing organic sedimentation because nitrogen normally acts as the primary limiting factor in algal growth (Berner 1990; Ravindran et al. 2012). Therefore, the observed spatial patterns are consistent with the hypothesis that higher-nutrient areas are more susceptible to opportunistic algal growth. Additionally, sites with more bleaching appear more vulnerable to algal opportunism. This could be either because the same factors act to promote both bleaching and algal growth, or because bleached sites provide a larger total area of exposed coral skeleton available to serve as a substrate.

Limitations of study and possible future directions

There are several considerable limitations to the scope of this study. First and foremost is the limited time period of data collection. Not only would a longer-term study result in a more extensive dataset, but it would also allow for temporal comparison. Bleaching and disease around Lokobe have been observed to fluctuate with the seasons, with more numerous and intense symptoms during the hot season, which runs from November to January (G. Bakary, *pers. comm.*, 5 Nov 2015). Greater intensity of disease has also been linked to high temperatures elsewhere (Bruno et al. 2007). Because this study was carried out during November, it's therefore possible that the rates of disease recorded were higher than the annual average. In any case, it would be interesting to quantify the seasonality of disease in this location specifically, especially given that yearly sea temperatures are increasing and expected to increase further in the near future (Goldberg and Wilkinson, 2004).

Snorkeling methodology also limited this study's survey range, mainly regarding reef depth. No areas of a depth over 4 meters were surveyed in this study, preventing the analysis of depth as a spatial driver (Table 1). Greater disease mortality rates have been observed in shallower waters elsewhere in the Indo-Pacific, specifically for white syndrome (Hobbs et al. 2015). Future surveys incorporating scuba diving could reveal whether this spatial pattern extends to Lokobe and surrounding areas.

It was also not possible to quantify sedimentary or chemical conditions of the water beyond the somewhat arbitrary turbidity estimate of "visibility." Therefore, many of the connections between health conditions and pollution or sediment in this study remain hypothetical. An investigation of whether the correlation between water quality and reef health found by Sheridan et al. (2014) in southeastern Madagascar extends to Nosy Be would be highly useful to local conservation efforts.

Finally, there appears to be more disease in the non-protected site of Nosy Komba, a result concurrent with existing literature on no-take zones (Lamb et al. 2015). That being said, this study was not intended as a comparison between protected and non-protected areas. [1] The data from Nosy Komba presented here is insufficient to conclude for certain whether the restricted-use zoning of Lokobe MPA is effective in limiting disease outbreaks. Future studies surveying compromised coral health in more non-restricted locations in comparison with Lokobe could better illuminate the relationship between official protection and disease.

Implications

Increasing global sea surface temperatures and ocean acidification are combining with the more local factors of coastal human habitation and fishing to seriously threaten coral reef health worldwide. It is crucial that reef conservation efforts take multiple scales of threats into account, as well as ecological patterns like those investigated here, when planning for the protection of these fragile ecosystems.

Hard coral genera are differentially sensitive to various health conditions, with *Acropora* especially vulnerable to bleaching and *Porites* most susceptible to multiple different diseases. These threats are especially serious considering that these two genera contain some of the most important reef-building corals (Longhurst and Pauly 1987). However, their differential susceptibility to threats offers some hope, in that an epidemic of one is not likely to wipe out both genera. A high level of biodiversity and more even species distributions would thus make a site more resilient in the face of disease outbreaks and bleaching events (Rogers 2013). Therefore, the management organizations

[1] See Deeg 2015 for a multi-factor comparison of fringing reef health in Lokobe MPA and Nosy Komba.

of protected reefs should make the preservation of biodiversity, and not just the maintenance of coral cover, a top priority.

While there were slight differences in spatial distribution between health conditions, corals closer to human habitation were more susceptible overall to bleaching, disease, and opportunistic colonization. Many environmental factors doubtless interact to produce this pattern. However, it is clear from this and previous studies that anthropogenic disturbances render coral more vulnerable to other stressors both directly and indirectly. It is therefore not enough to focus conservation efforts only on marine areas: even if no-take or restricted-use zones are established that protect reefs from fishing, thermal and water quality stressors will still threaten coral health. One popular recommendation for reef managers is a “ridge-to-reef” approach that takes upstream ecological influences into account (Rogers 2013). Protected areas like Lokobe, which combines terrestrial and marine zones, are therefore crucial in the ongoing effort to preserve fringing reef health.

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APPENDIX

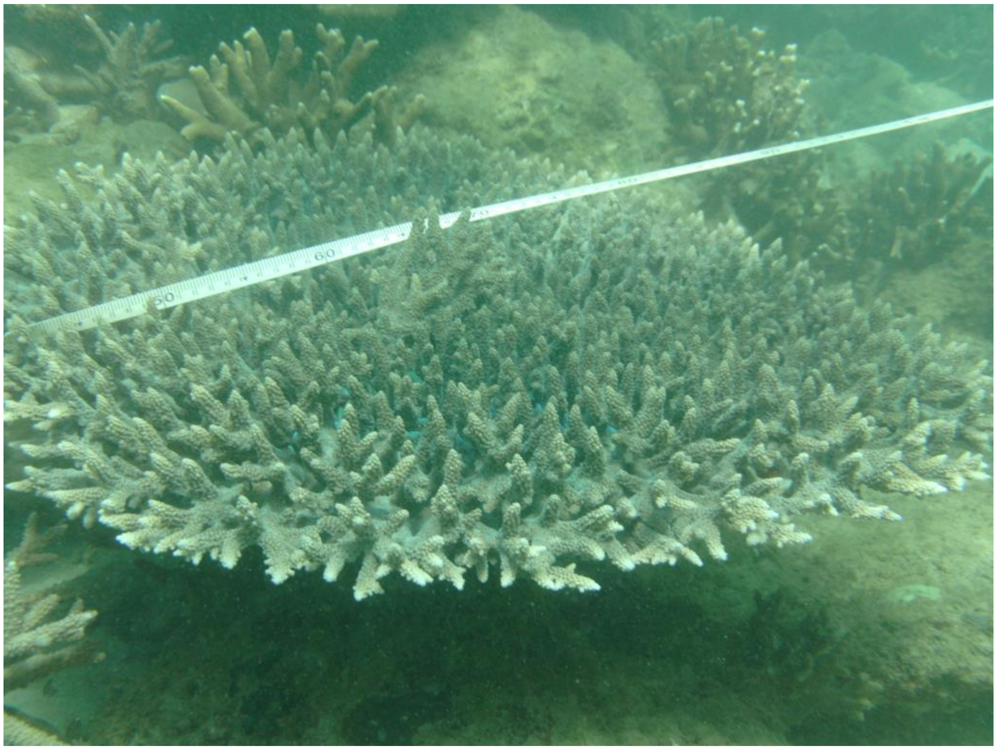

Fig. 11. *Acropora hyacinthus*, a plate coral, with tape measure marking the belt transect. Image courtesy of Gisèle Bakary.

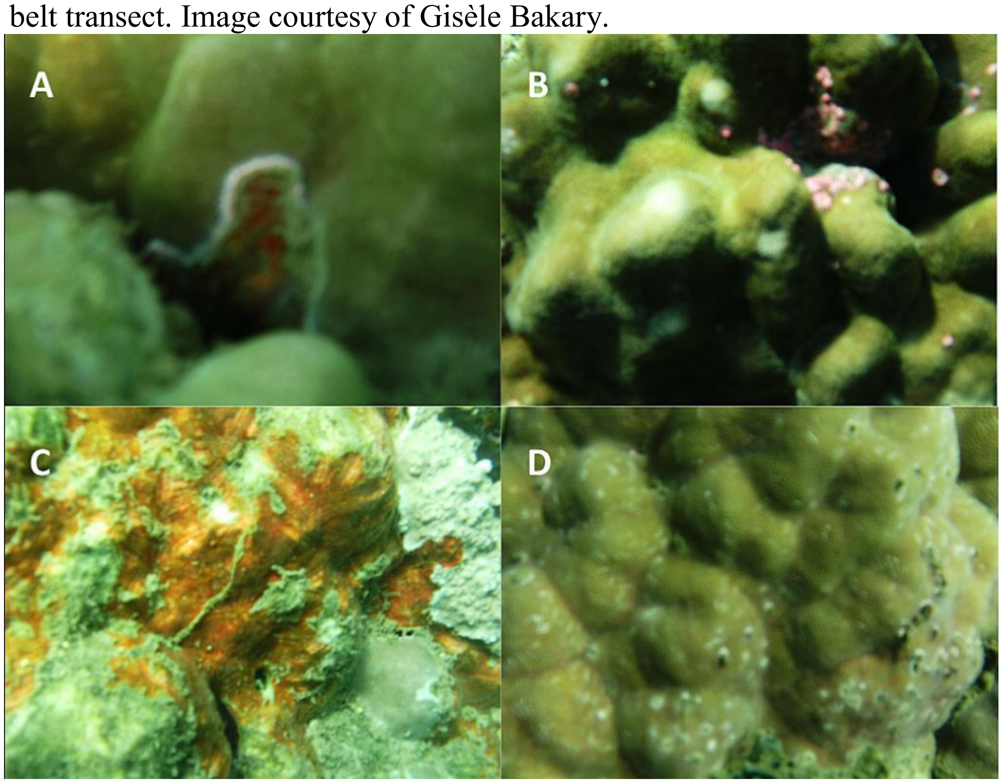

Fig. 12. Different coral diseases of *Porites* hard corals. A: white syndrome (WS). B: pink spot (PS). C: orange band (OB). D: *Porites* ulcerative white spot (PUWS).